THE EMBRYOLOGY AND RELATIONSHIPS OF *ALZATEA* RUIZ & PAV. (ALZATEACEAE, MYRTALES)[1]

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ABSTRACT

In this paper we present the first embryological studies of *Alzatea,* one of the genera of the order Myrtales whose placement has been most controversial. Although *Alzatea* agrees rather completely with the other Myrtales in its basic embryological characteristics, it stands apart from all other members of the order that have been examined in having a bisporic *Allium*-type embryo sac. Comparisons with related groups, including *Axinandra, Rhynchocalyx,* Lythraceae, and Melastomataceae, indicate that *Alzatea* shares many more characteristics with *Rhynchocalyx* than with the others. Among the groups mentioned, only *Alzatea* and *Rhynchocalyx* coincide in their micropyle form, and both genera further agree with Lythraceae in the multi-celled ovule archesporium, which is not known elsewhere in the order except in one of the small subfamilies of Lythraceae, Sonneratioideae. A totality of similarities and dissimilarities with the other Myrtales favors the establishment of a monotypic family, Alzateaceae, and suggests that *Alzatea* and *Rhynchocalyx* may be parallel descendants from a common ancestor, with which the modern Lythraceae possibly has a link.

This paper deals with the embryology of the rare monotypic Central-South American genus, *Alzatea,* and is the third concerning the unique genera of the order Myrtales, following papers on *Axinandra* (Tobe & Raven, 1983b) and *Rhynchocalyx* (Tobe & Raven, 1984). As in the case of *Axinandra* and *Rhynchocalyx,* there has been a long history of arguments about the taxonomic position of *Alzatea.* According to Lourteig (1965), who gave a historical review up to that time, *Alzatea* has been placed in Celastraceae (De Candolle, 1825; Bentham & Hooker, 1862), Rhamnaceae (Miers, 1872; Loesener, 1942; MacBride, 1951), and Lythraceae (Planchon, 1845; Hallier, 1911; Pilger, 1915). Lourteig (1965) herself concluded that *Alzatea* belonged in Lythraceae, based on its floral and vegetative characters as well as on anatomical and palynological characters. She considered the genus to be a member of subtribe Diplusodontinae of tribe Lythreae.

At other times in its history, *Alzatea* has been considered to have a close affinity with another unique genus, *Crypteronia,* regardless of the family to which *Crypteronia* was assigned at that time (Miers, 1872; Loesener, 1942). Recently, van Beusekom-Osinga and van Beusekom (1975) proposed broadening the definition of Crypteroniaceae to include *Alzatea* together with *Crypteronia, Dactylocladus, Axinandra,* and *Rhynchocalyx.* Muller (1975) suggested a possible relationship among these five genera based on their pollen morphology. But van Vliet (1975), van Vliet and Baas (1975), and Baas (1979), on the basis of their studies of the wood, leaf, twig, and nodal anatomy, suggested not only that *Alzatea* and *Rhynchocalyx* differed widely from the three other genera of Crypteroniaceae sensu lato, but also that these two genera differed to a substantial degree from each other. Dahlgren and Thorne (1984) and Johnson and Briggs (1984) accepted the establishment by S. Graham (1984) of a monotypic family, Alzateaceae.

Results of our recent embryological studies have indicated that *Axinandra* and *Rhynchocalyx* are very different from each other, and that the former occupies a satellite position to Melastomataceae (Tobe & Raven, 1983b, 1984). *Rynchocalyx* is of less certain placement, but probably deserves the family status that it was accorded by Johnson and Briggs (1984). We carried out the present study of the embryology of *Alzatea,* which has hitherto been unknown, as a contribution to determining its most appropriate systematic position.

MATERIALS AND METHODS

The only species of what is probably a monotypic family, *Alzatea verticillata* Ruiz & Pav.,

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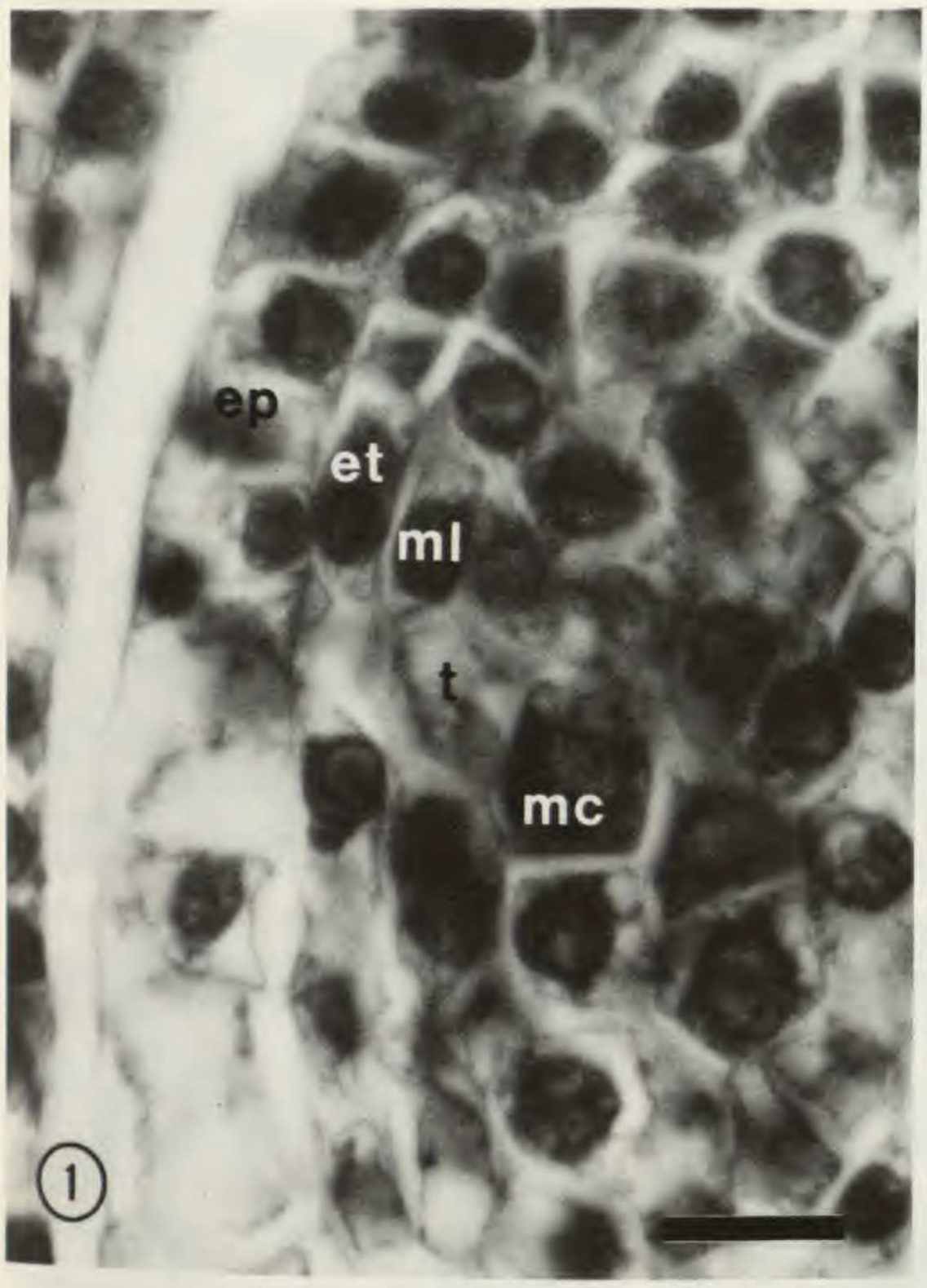
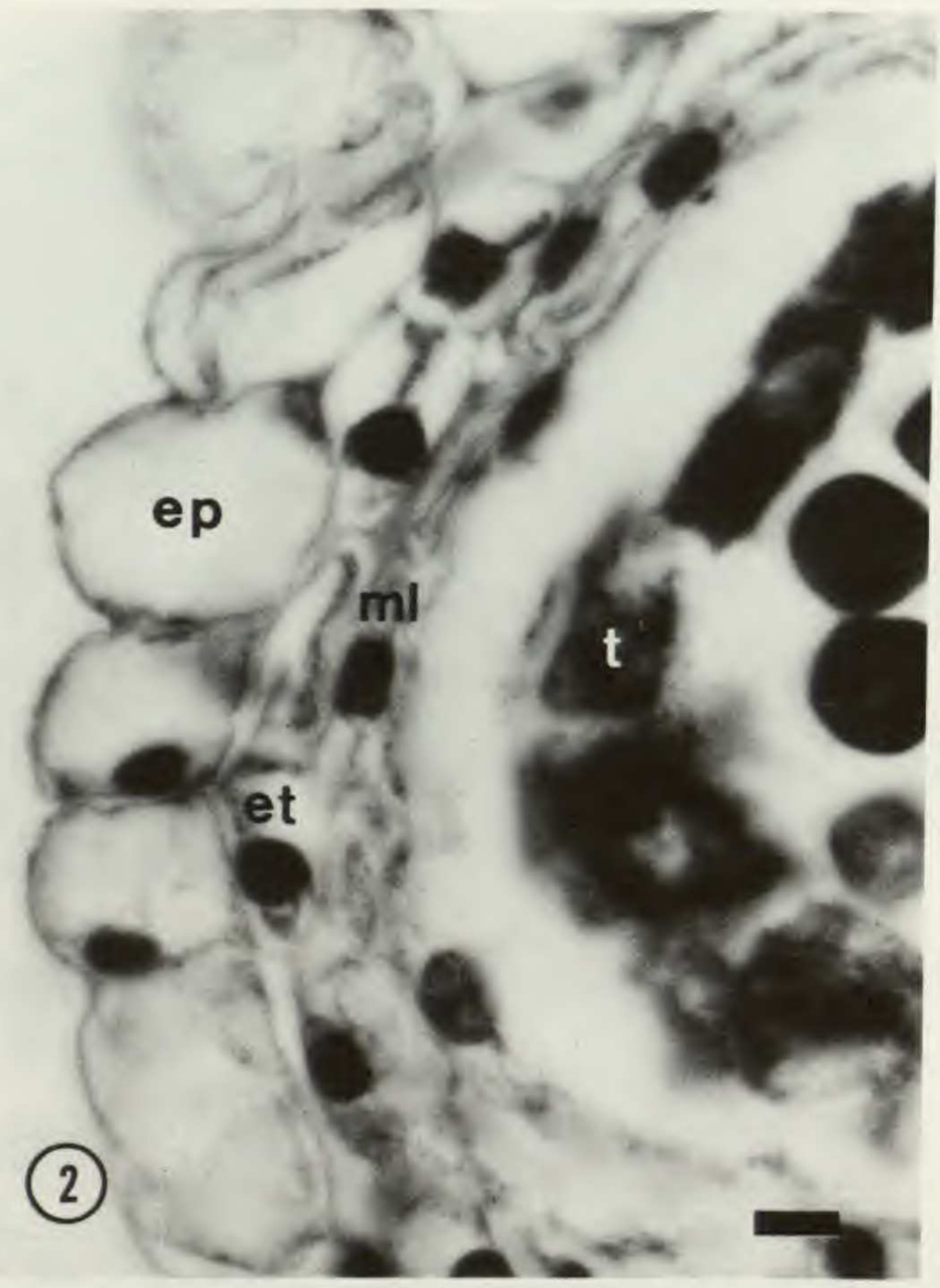
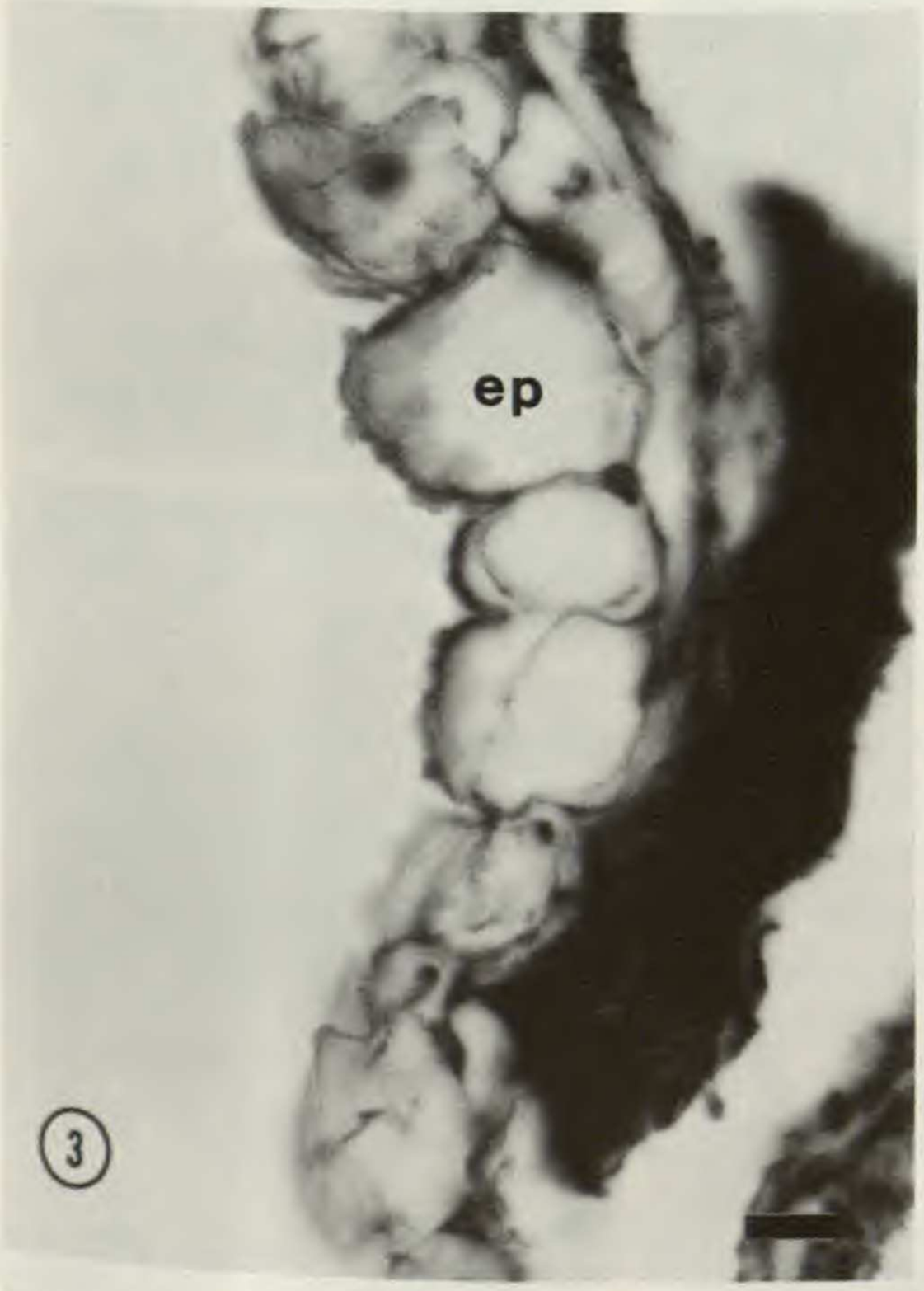
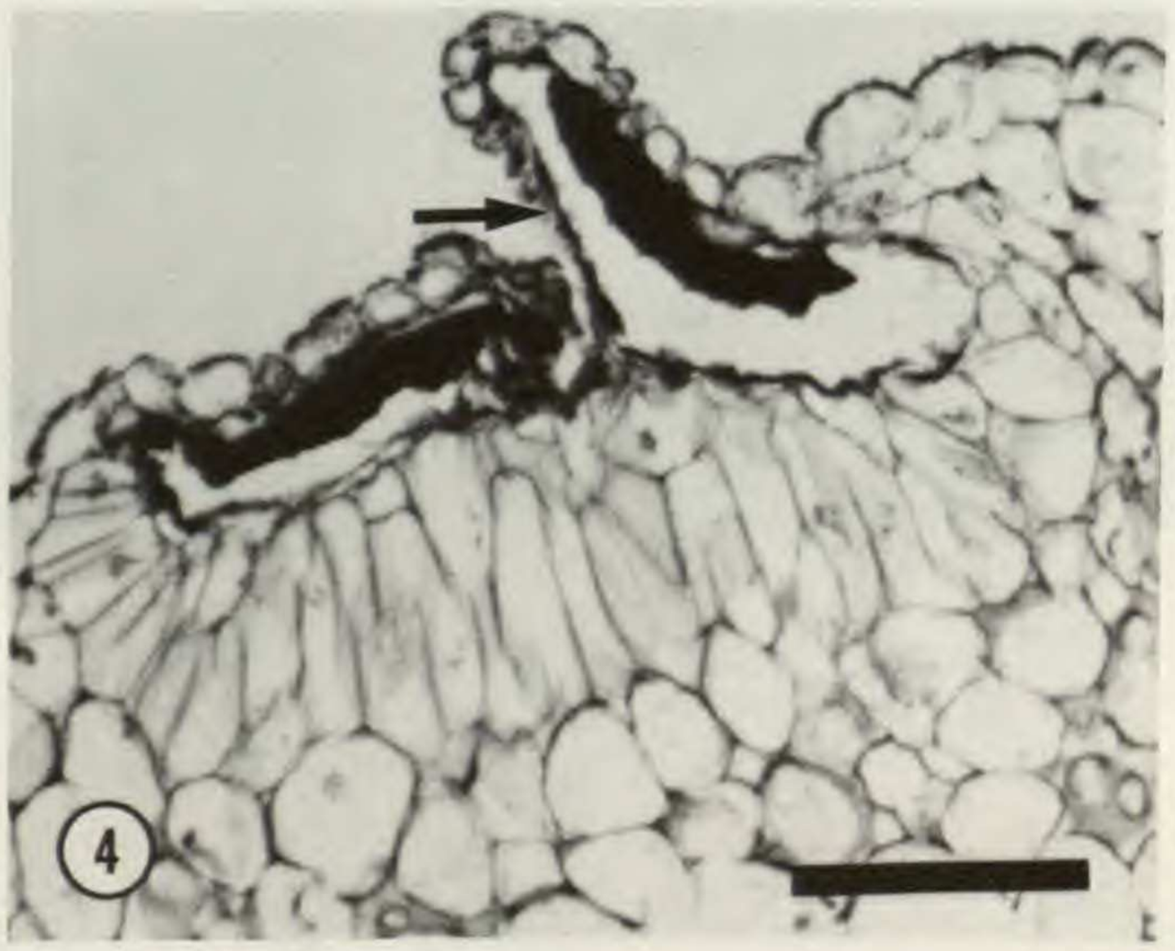
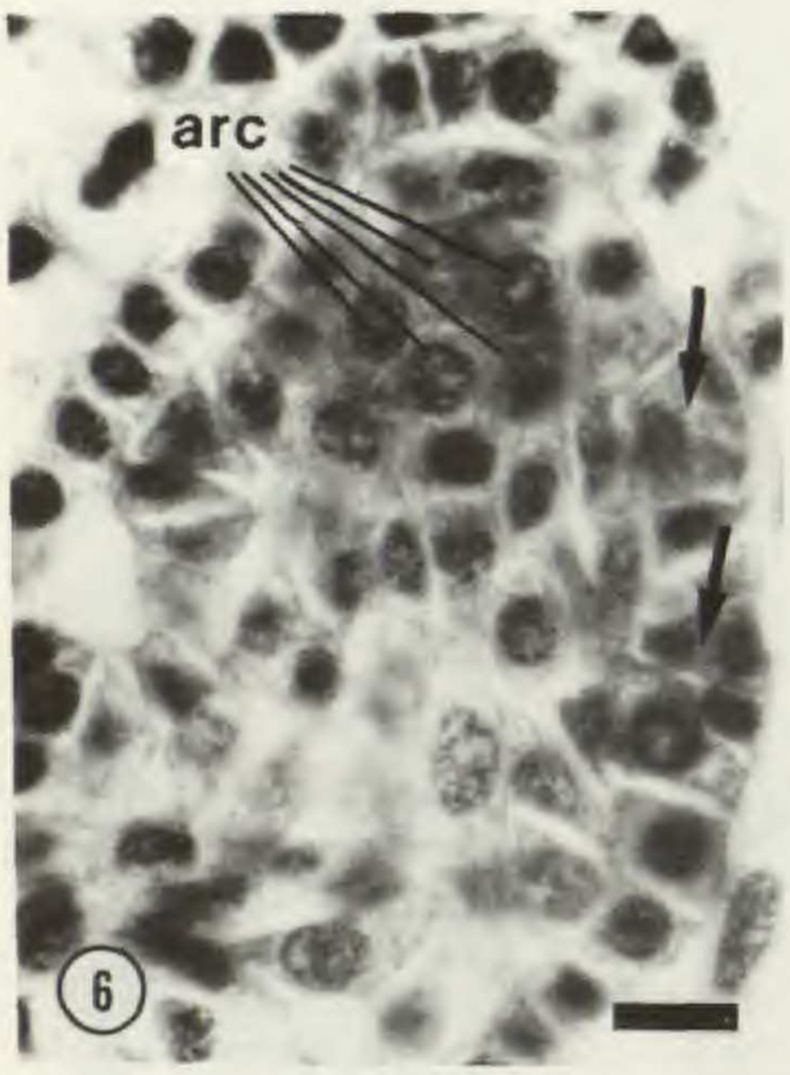


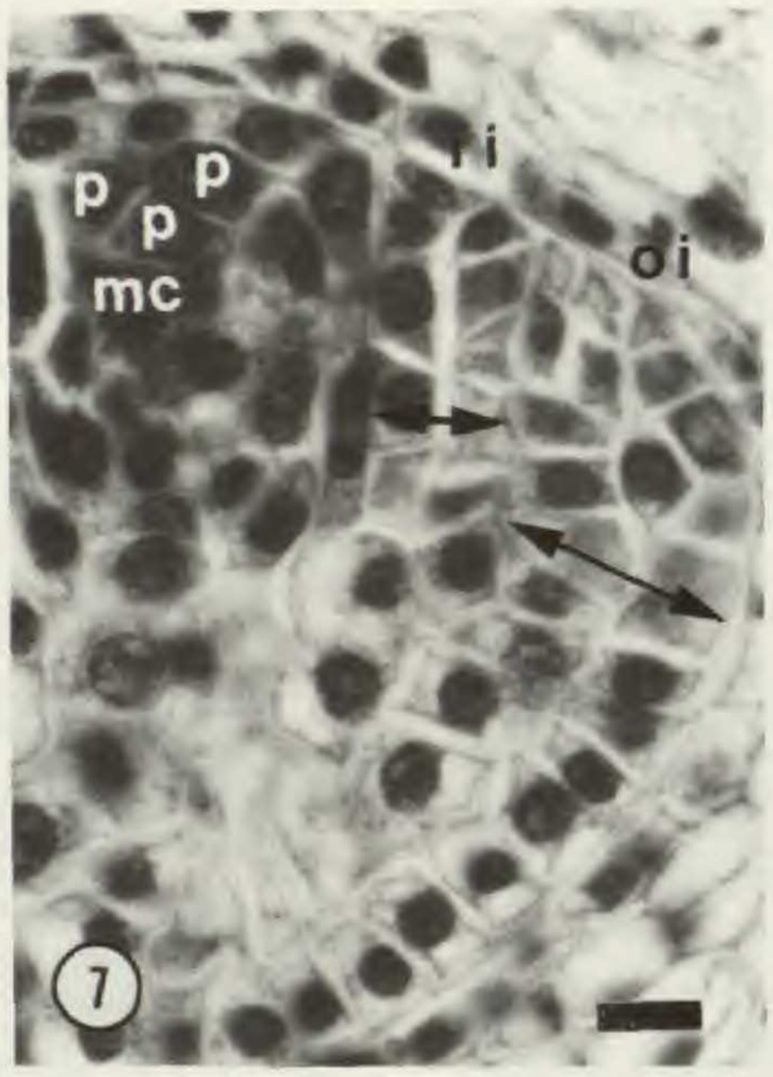


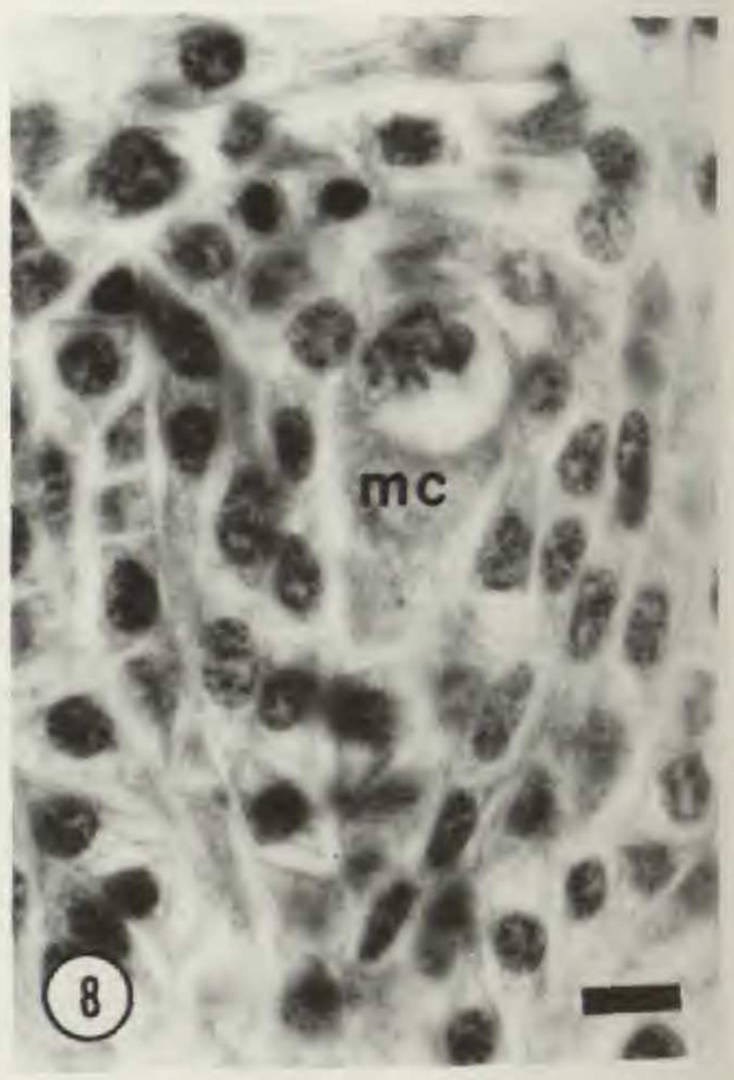


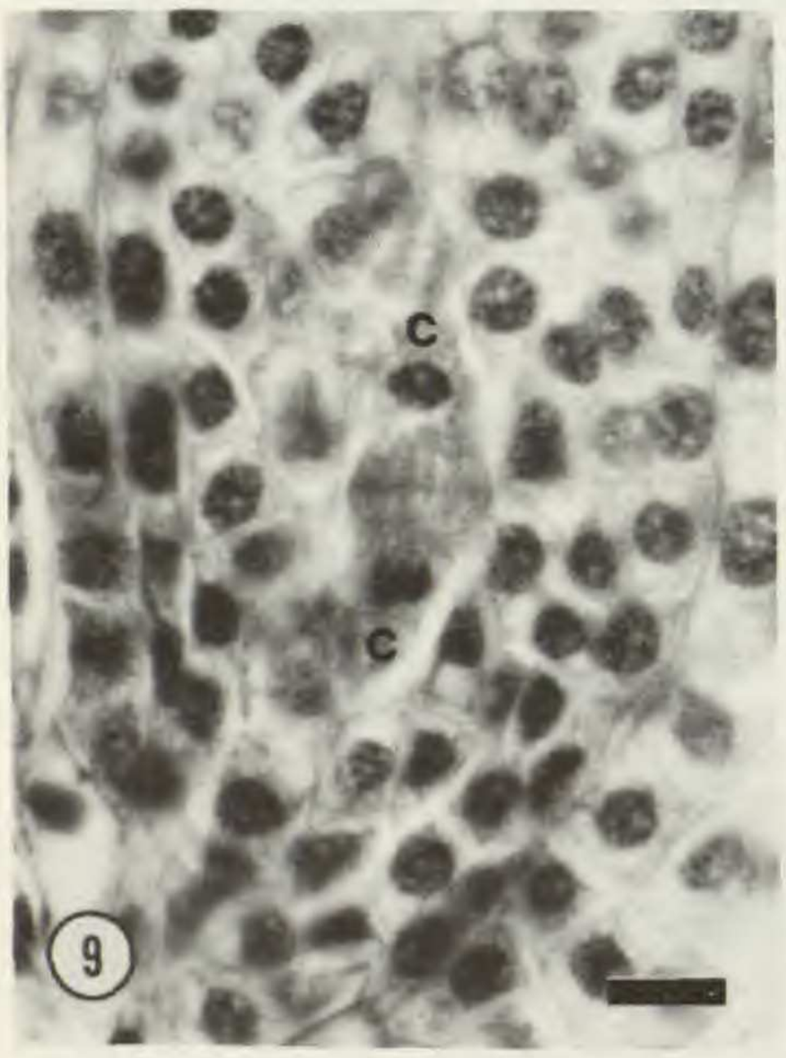


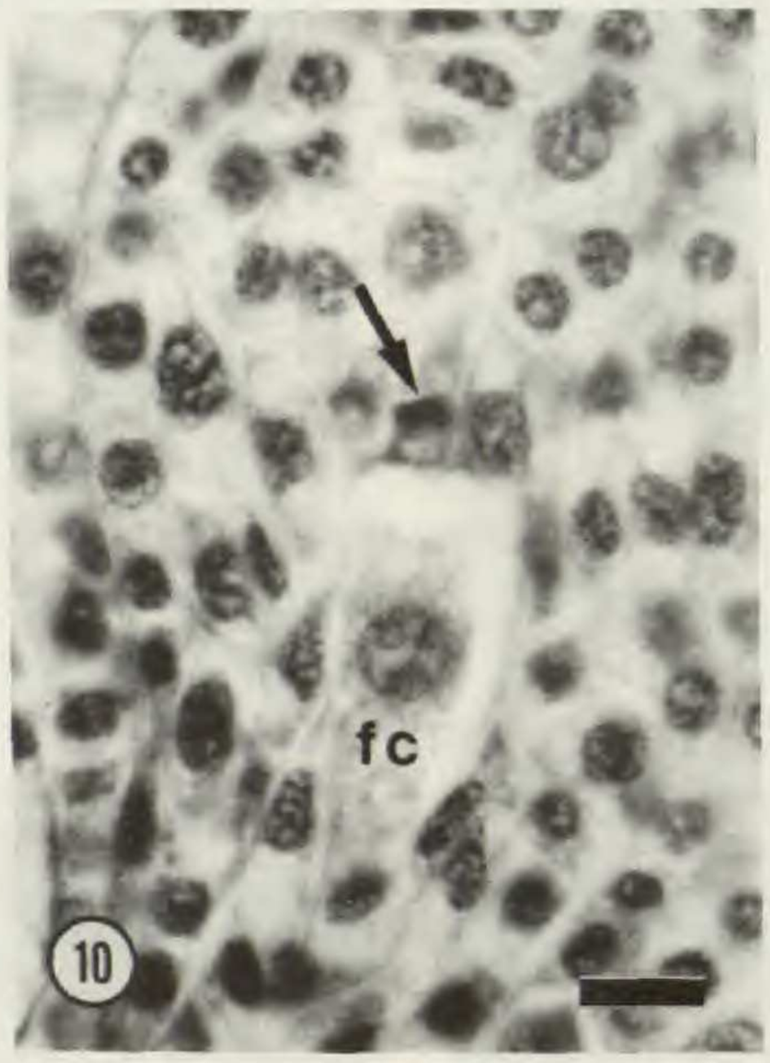
FIGURES 1–5. —1. Transverse section of a young anther. Its wall is formed by an epidermis (*ep*), an endothecium (*et*), a middle layer (*ml*) and a tapetum (*t*), inside the last of which microspore mother cells (*mc*) are produced. Bar = 10μm.—2. Cross-section of an older anther. The epidermal cells (*ep*) are enlarged while the endothecium (*et*), the middle layer (*ml*) and the tapetum (*t*) are degenerating. Bar = 10 μm.—3. Cross section of a mature anther, showing a persistent epidermis (*ep*). Bar = 10 μm.—4. Cross section of the mature anther. An arrow indicates the degenerating septum between two microsporangia. Bar = 100 μm.—5. Two-celled pollen grains at the time of shedding. Arrows point out nuclei of a generative and a vegetative cell. Bar = 10 μm.

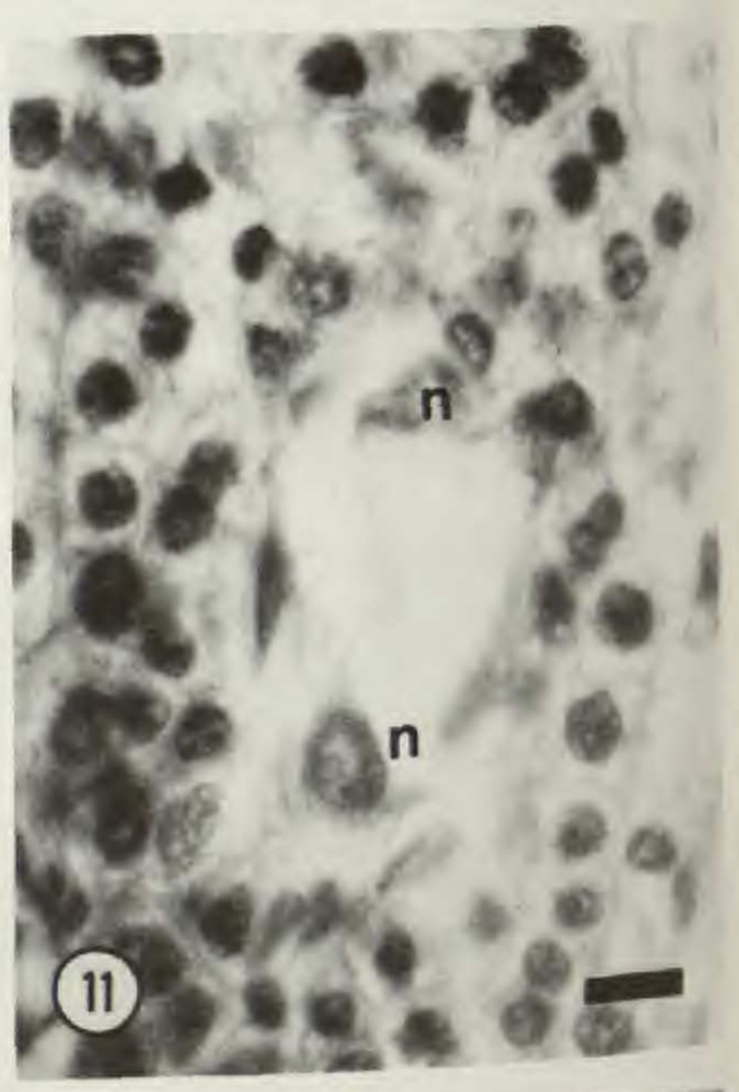


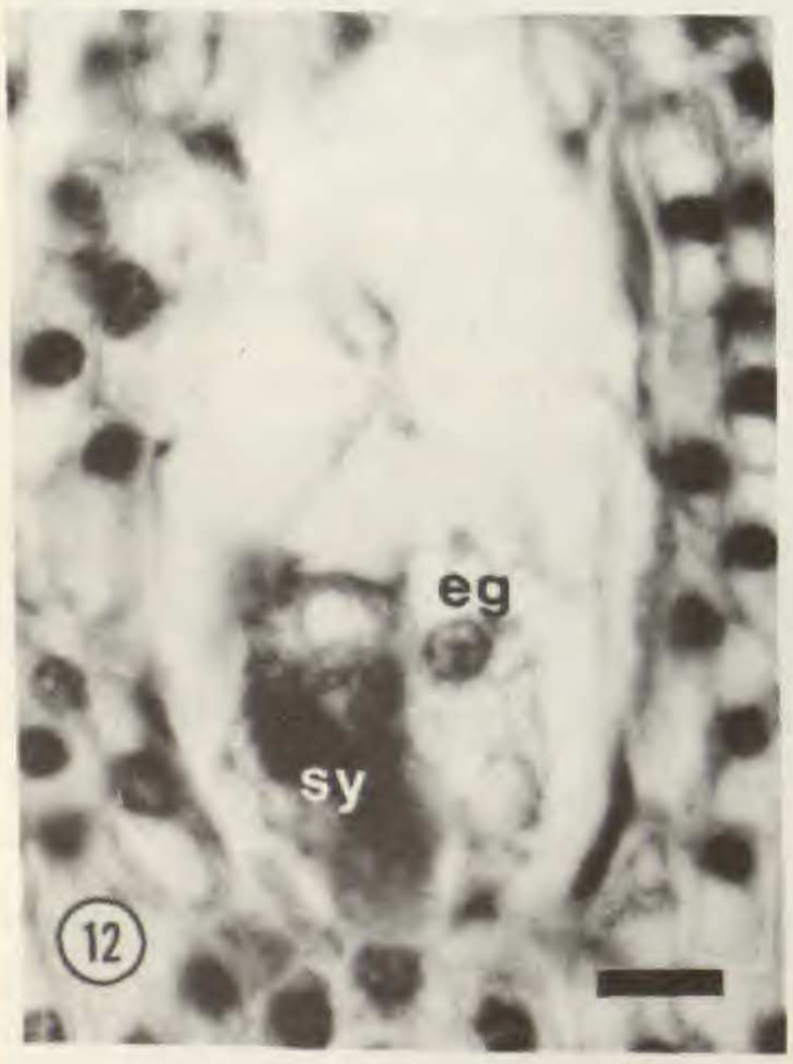


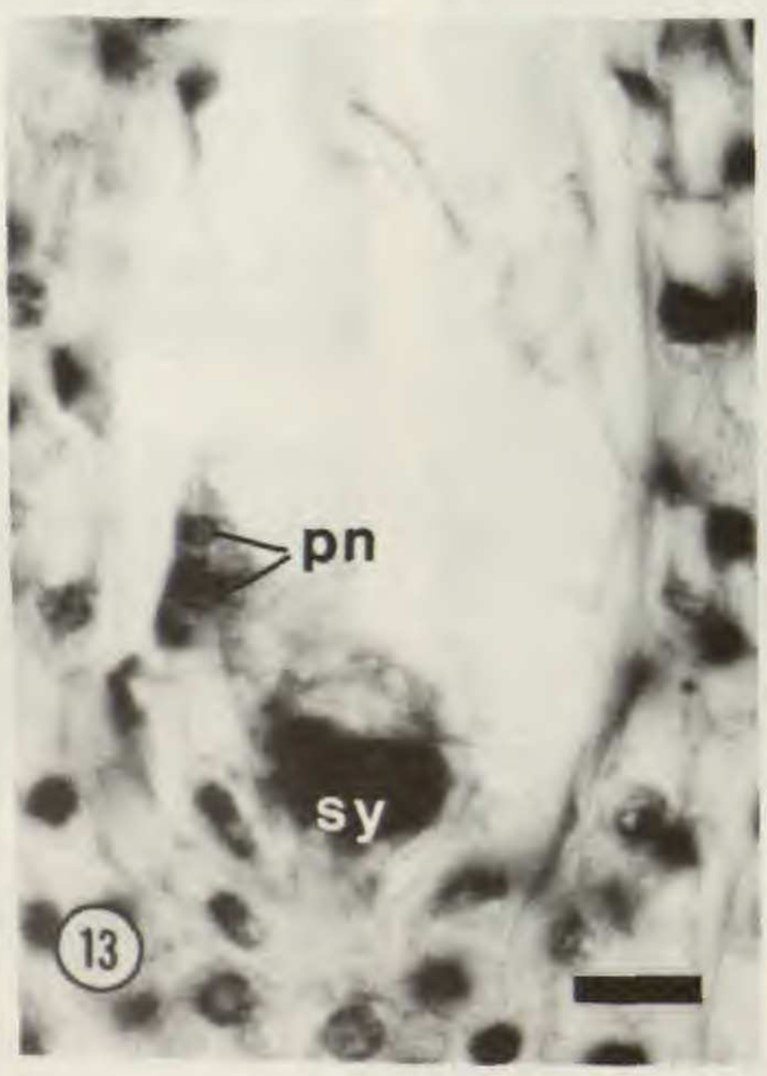


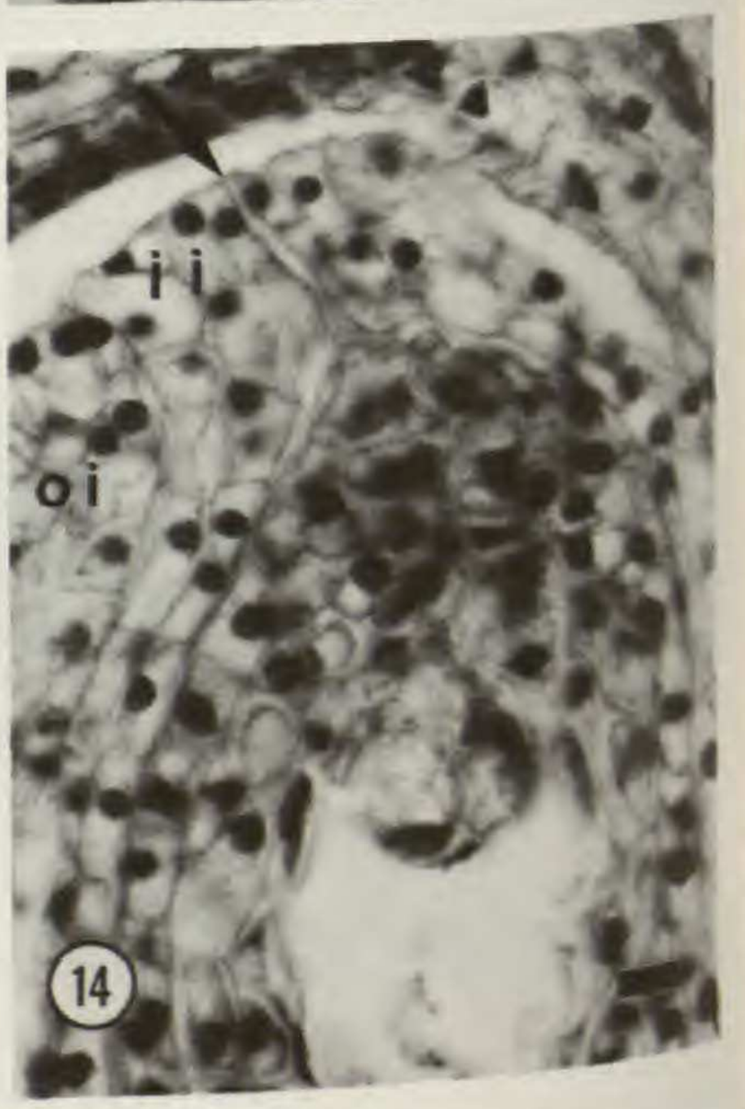












FIGURES 6–14. —6. Longitudinal section of an ovule primordium with a multicelled archesporium. Arrows indicate periclinal divisions of the dermal initial cells of the inner and the outer integument. Archesporial cell (*arc*). Bar = 10 μm.—7. Longitudinal section of a young ovule with two growing integuments. Note that both the inner (*ii*) and the outer (*oi*) integument are two-layered in their original thickness. Only one of the archesporial cells functions to form parietal cells (*p*) and a single megaspore mother cell (*mc*). Bar = 10 μm.—8. Longitudinal

was examined in this study. Most of our observations were based on flower buds and fruits collected in Panama (voucher specimens: *Knapp 4336, 4087,* MO; *Knapp & Dressler 5392,* MO), supplemented, particularly with respect to mature seed morphology and anatomy, with material collected in Costa Rica (voucher specimen: *Poveda 3264,* MO). Both samples were fixed and preserved with FAA (five parts stock formalin: five parts glacial acetic acid: 90 parts 70% ethanol). Preparations of microtome sections were made following a technique described in a previous paper (Tobe & Raven, 1983b).

All of our flower samples from Panama (*Knapp 4336, 4087, Knapp & Dressler 5392*) have produced only sterile pollen sacs which have either crushed sporogenous tissues or, at most, aberrant pollen grains. Therefore, a different herbarium specimen from Peru (*Woytkowski 8331,* MO) was used for the observation of the shape of microspore tetrads and of the cell number of mature pollen grains. Pollen grains stained with 1% acetocarmine gave good results in counting the cell numbers in a few hours.

Observations

Anther and microspores

The anther is tetrasporangiate. The wall structure prior to maturation comprises four layers, i.e., an epidermis, an endothecium, a middle layer, and a tapetum (Fig. 1). Since the endothecium and the middle layer have a common origin histogenetically, the wall formation is regarded as conforming to the Dicotyledonous type (Davis 1966: 10). During the process of maturation, the epidermal cells are enlarged while both the endothecium and the middle layer degenerate (Fig. 2). Consequently, the mature anther wall is composed only of the persistent epidermis, each of the epidermal cells being greatly enlarged (Fig. 3), and the cells of the connective tissue adjacent to pollen sacs are radially elongated (Fig. 4). The tapetum is glandular, and its cells become two-nucleate before they degenerate. A septum between two microsporangia on each side of the anther is broken down as is usual in angiosperms (arrow, Fig. 4).

The shape of microspore tetrads, on the basis of the examination of 20 selected tetrads, is "usually" (65%) tetrahedral and "often" (35%) decussate (expressions for the frequency follow Schmid, 1982). Pollen grains are two-celled at the time of shedding (arrows, Fig. 5).

Curiously, although pollen from Peru (*Woytkowski 8331,* MO) was 97% stainable, that of a collection from Costa Rica (*Dryer 941,* CR) was only about 31% stainable, and we have seen no fertile pollen in collections from Panama. These points clearly merit further investigation.

Megagametophyte and nucellus

The ovule is anatropous and crassinucellate. An archesporium is hypodermal. Four to eight archesporial cells are differentiated from the other somatic cells (Fig. 6). Only one of them divides further, periclinally into two: the upper primary parietal cell and the lower sporogenous cell. The primary parietal cell divides once periclinally or anticlinally and both cells repeat periclinal and anticlinal divisions to form a massive parietal tissue (Fig. 7). The sporogenous cell develops into a megaspore mother cell (Fig. 8). After enlarging in volume, the megaspore mother cell undergoes meiosis to form a linear dyad of megaspores (Fig. 9). The upper micropylar megaspore of the dyad soon degenerates (arrow, Fig. 10), while the lower chalazal megaspore functions (Fig. 10). This functional megaspore involves three successive nuclear divisions, resulting in two- (Fig. 11), four-, and eight-nucleate embryo sacs. Thus the embryo sac formation conforms to the bisporic *Allium*-type. Synergids are pyriform (Figs. 12, 13), and antipodals are very ephemeral and disappear before fertilization. An organized mature embryo sac just before fertilization is composed of five nuclei or cells: an egg cell, two synergids, and two polar

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section of a young ovule with a single enlarged megaspore mother cell (*mc*). Bar = 10 μm.—9. Longitudinal section of a young ovule showing a dyad of megaspores (*c*). Bar = 10 μm.—10. Longitudinal section of a young ovule with a functional megaspore (*fc*) of the dyad enlarging. An arrow indicates a degenerated micropylar megaspore of the dyad. Bar = 10 μm.—11. Longitudinal section of a young ovule with a two-nucleate embryo sac. Nucleus in the embryo sac (*n*). Bar = 10 μm.—12, 13. Two successive longitudinal sections of a mature ovule with an organized mature embryo sac. Egg cell (*eg*); synergid (*sy*); polar nucleus (*pn*). Bar = 10 μm.—14. Longitudinal section of a mature ovule with an organized mature embryo. Note that the micropyle (at arrow) is formed by the inner integument (*ii*) alone. Outer integument (*oi*). Bar = 10 μm.

nuclei (Figs. 12, 13). Both the nucleus and the nucleolus of the egg cell are much smaller than those of synergids (Fig. 12).

During megasporogenesis and megagametogenesis, the nucellar tissue does not show any particular differentiation.

INTEGUMENTS

The ovule is bitegmic. Both the inner and the outer integument are initiated by periclinal divisions of dermal cells of the ovular primordium (arrows, Fig. 6); they grow only by divisions of the cells derived from the dermal initial cells. The growing inner integument is consistently two-layered and keeps its original thickness in the later stages as well. The outer integument also has a two-layered structure at the initiation stage but soon increases in thickness because of anticlinal divisions of the constituent cells, resulting in a two- to four-layered structure (Fig. 7). This multiplication is most conspicuous in those portions of the integument along the equatorial line of the ovules, which are horizontally placed in an ovarian locule, and represents the first sign of the formation of the seed wing.

The inner integument elongates more than the outer one. As a result, the micropyle is formed by the inner integument alone (Fig. 14).

EMBRYO AND ENDOSPERM

Since we could not locate the remnants of pollen tubes in microtome sections of fruit samples from Panama (*Knapp & Dressler 5392*), we are not certain whether the egg cell was actually fertilized in these samples or not. We did, however, encounter a fair number of proembryos in this collection. Based on our studies of these proembryos, embryogenesis apparently occurred normally until at least the globular proembryonal stage, and conforms to the Onagrad type. The apical cell of a two-celled proembryo divides vertically, and the basal cell transversely (Fig. 15). In an older proembryo, the upper globular portion is formed by cells derived from the apical cell at the two-celled proembryonal stage, while the lower part including the suspensor is formed by cells derived from the basal cell (Fig. 16). An embryo in a mature seed (from the sample collected in Costa Rica) has two equally developed cotyledons and a short and small suspensor. The cotyledons are not folded (Fig. 19).

Endosperm formation is of the Nuclear type (Fig. 16), although, as mentioned above, there is some doubt that fertilization actually occurred in these samples. The endosperm is very scanty throughout the seed development. Only about ten nuclei are observed even at the four-celled proembryonal stage. The endosperm does not show any accumulation of free nuclei in the chalazal region or in the micropylar region. Probably wall formation does not occur in free endosperm nuclei. The mature seed completely lacks endosperm (Fig. 17).

MATURE SEED AND SEED COAT

The mature seed has a membranous wing with the embryo centered (Figs. 18, 19). Its shape and size are diverse, depending on the degree of development of the wing. The wing is formed by tissues of both the funiculus and the outer integument along the horizontal line of the seed, and is composed mostly of undulating epidermal cells (Fig. 20). A hypostase is formed by the time the embryo sac is mature, but it does not become conspicuous even in the mature seed (Fig. 18).

The mature seed coat is thin except for a part of the wing, and it is made up mainly from the elongate outer epidermal cells of the testa. The inner epidermis and, if present, the mesophyll of the testa, as well as the inner and the outer epidermis of the tegmen, completely collapse, leaving only their cell walls when the seed is mature (Fig. 17).

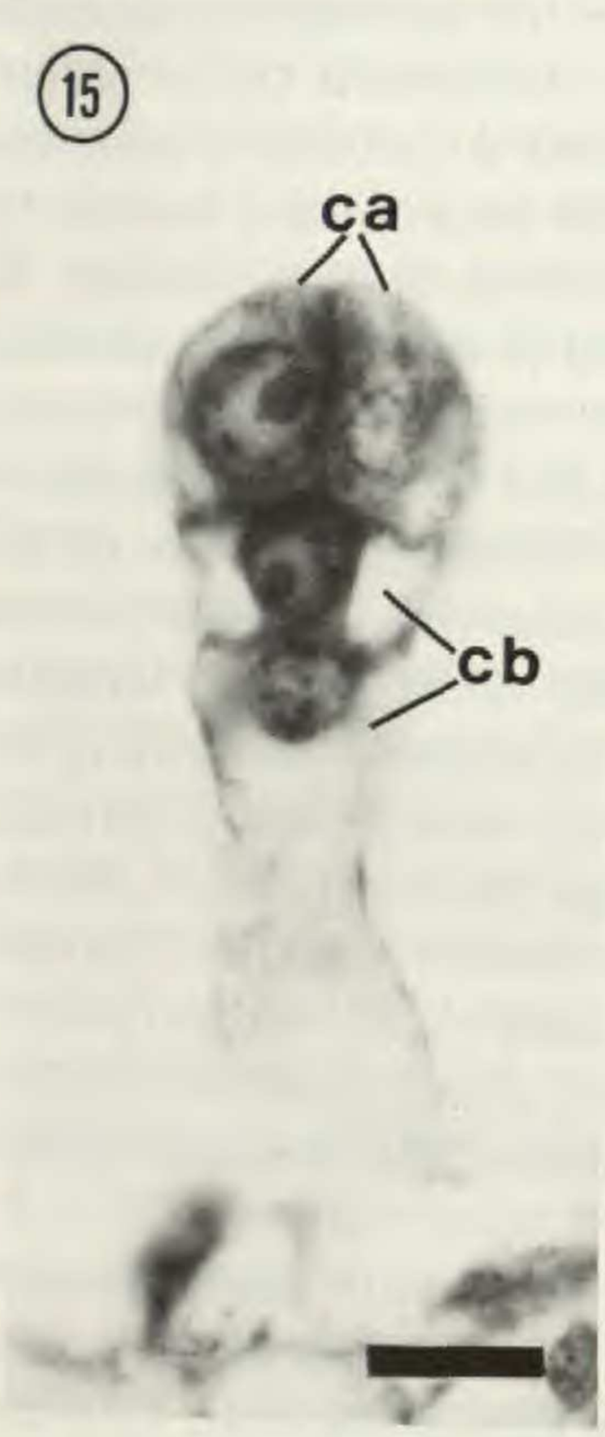
DISCUSSION

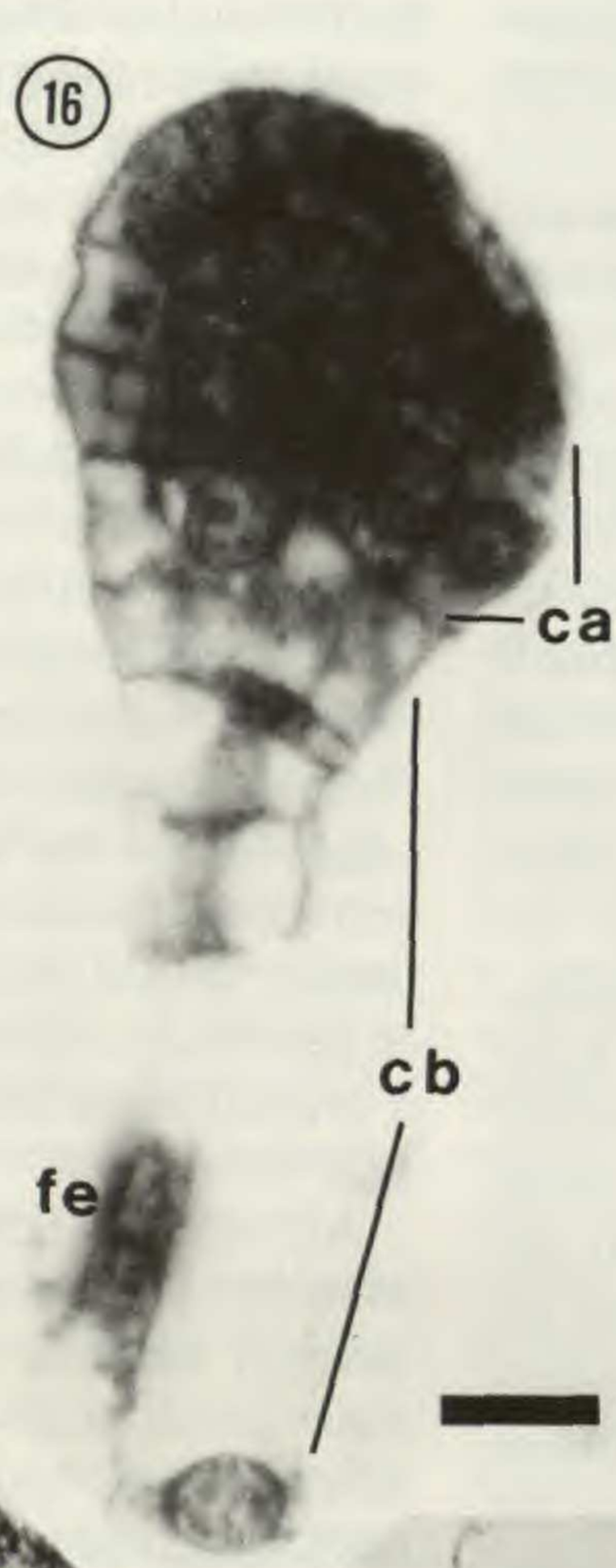
The embryological characteristics of *Alzatea verticillata* may be summarized as follows:

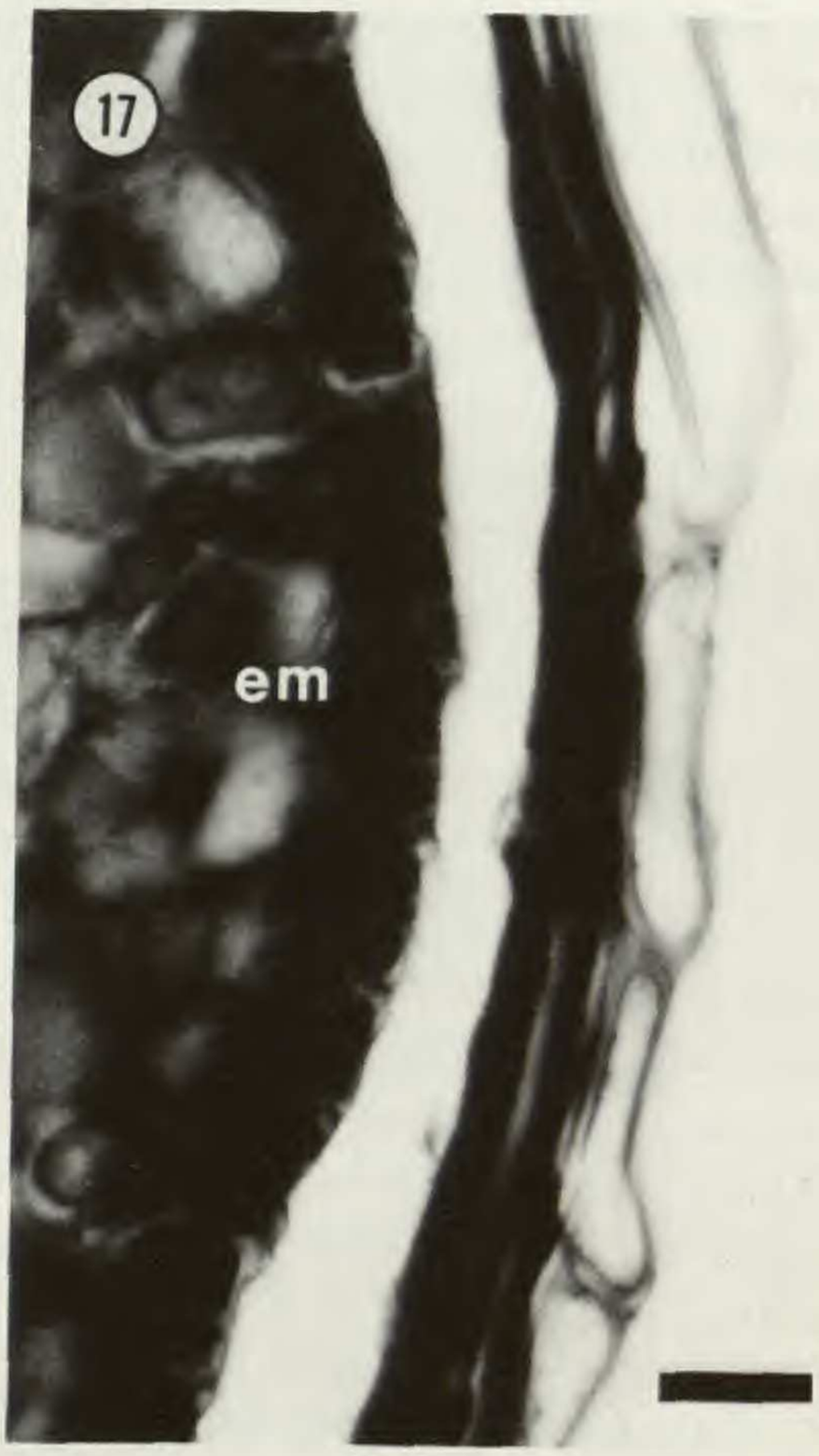
Anther tetrasporangiate; anther wall four layers thick, its formation of the Dicotyledonous type; anther epidermis persistent; both endothecium and middle layer ephemeral; tapetum glandular, its cells two-nucleate; septum between two microsporangia on each side of the anther collapsed; microspore tetrads tetrahedral or decussate; pollen grains two-celled when shed.

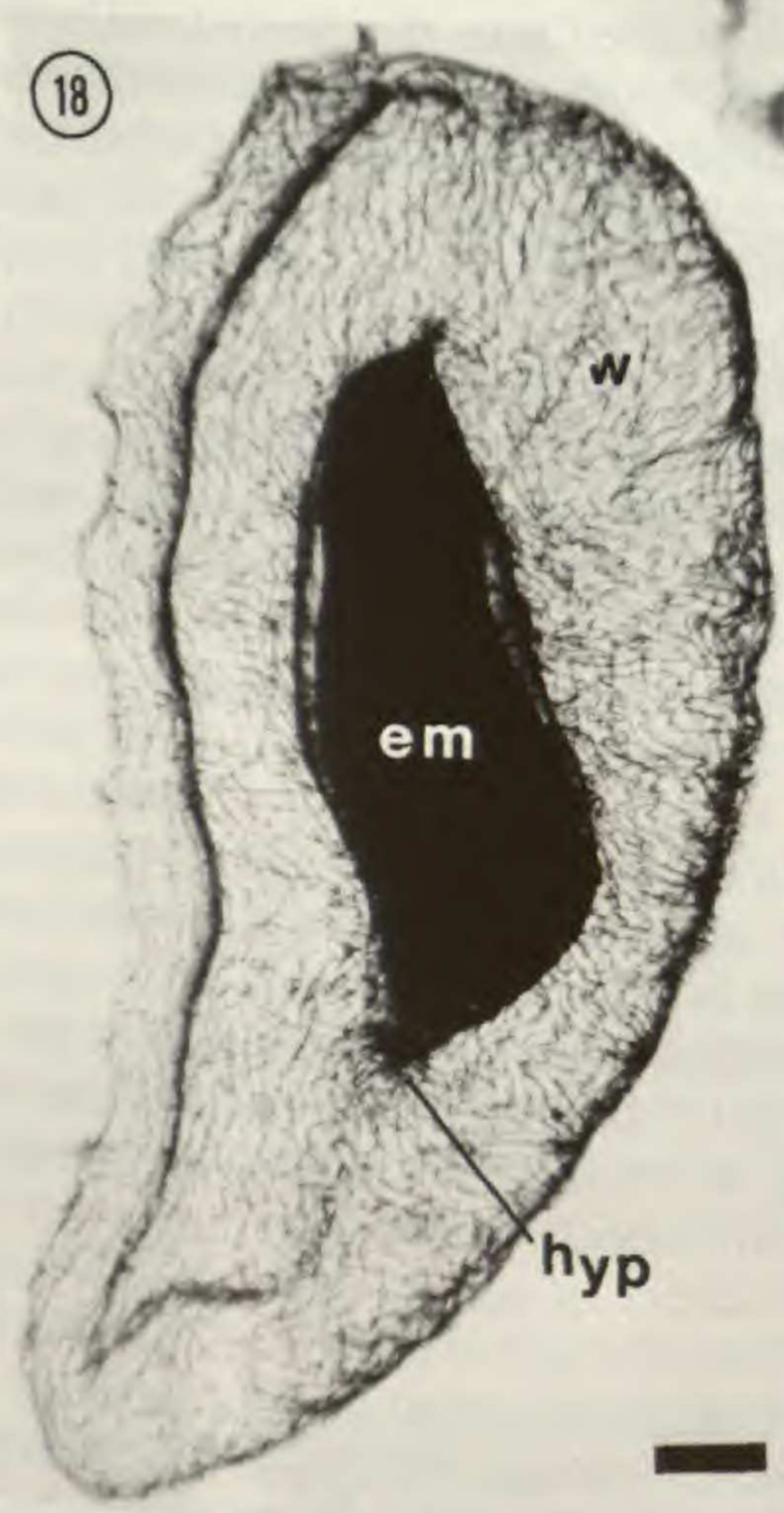
Ovule anatropous, bitegmic, and crassinucellate; both integuments initially two-layered, but later the outer integument two to four layers thick; micropyle formed by the inner integument alone; chalaza with hypostase.

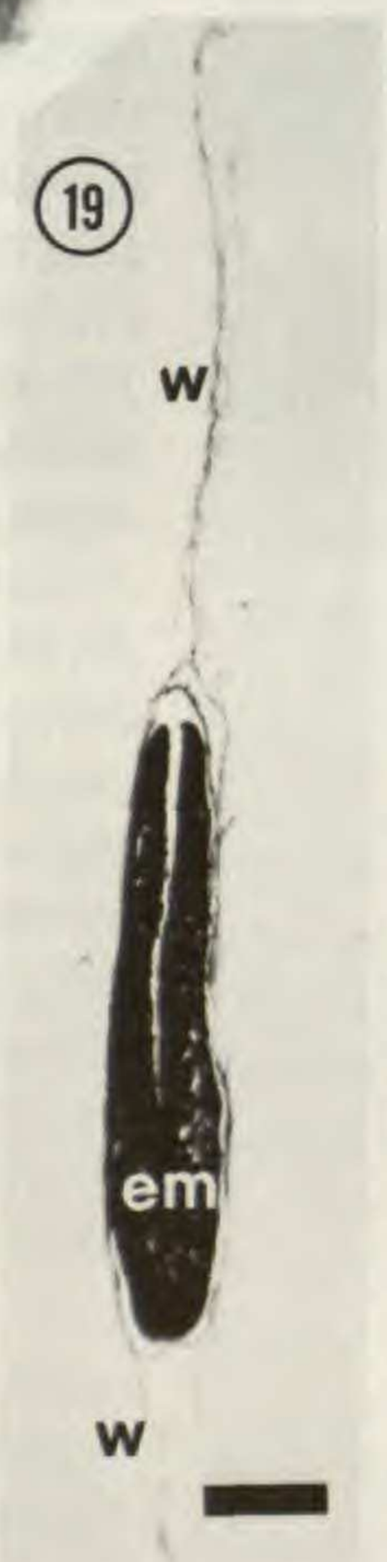
Archesporium of ovule multicelled, comprising four to eight cells, only one of them functioning and cutting off a primary parietal cell; meiosis in the megaspore mother cell forming a linear dyad of megaspores; micropylar megaspore of the dyad degenerating; the chalazal

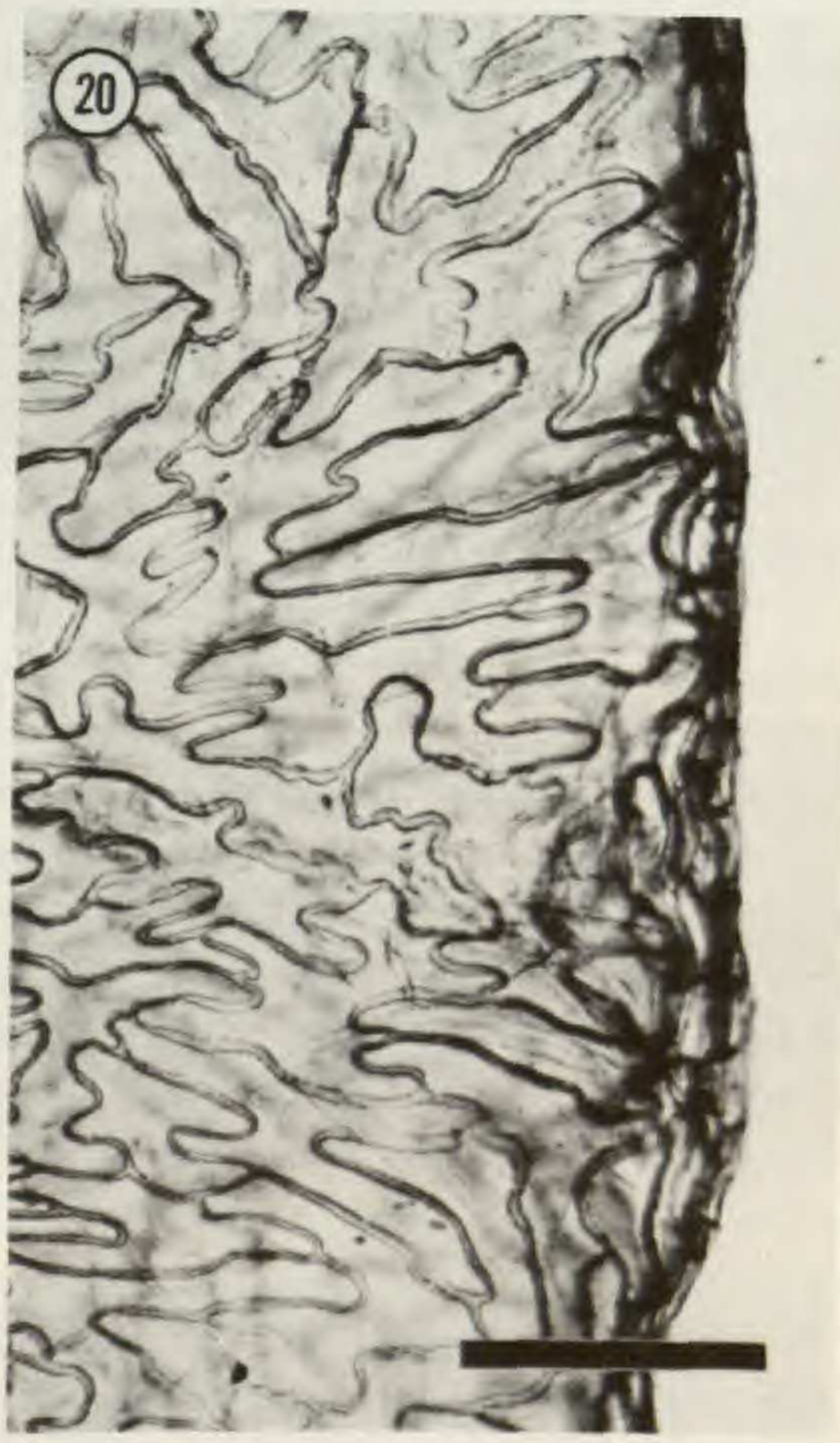












FIGURES 15–20. —15. Longitudinal section of a four-celled proembryo. Cells derived from an apical cell at the two-celled proembryonal stage (*ca*); cells derived from a basal cell (*cb*). Bar = 10 μm.—16. Longitudinal section of a globular proembryo. Cells derived from the apical cell at the two-celled proembryonal stage (*ca*); cells derived from the basal cell (*cb*); free endosperm nucleus (*fe*). Bar = 10 μm.—17. Cross section of a mature seed. Endosperm is absent. Note that a mature seed coat is composed of elongate outer epidermal cells of the testa as well as of walls of crushed cells of the other layers. Embryo (*em*). Bar = 10 μm.—18. Mature seed with a flat membranous wing (*w*). Embryo (*em*); hypostase (*hyp*). Bar = 200 μm.—19. Longitudinal section of a mature seed. Wing (*w*); embryo (*em*). Bar = 200 μm.—20. Part of the wing. Note the undulating epidermal cells constituting the wing. Bar = 100 μm.

megaspore developing into a bisporic eight-nucleate *Allium*-type embryo sac; antipodals ephemeral.

Endosperm formation Nuclear type; free endosperm scanty throughout seed development; mature seed exalbuminous; embryogenesis conforming to the Onagrad type; embryo dicotyledonous with a short and small suspensor; mature seed with a flat membranous wing along the horizontal line of the seed; wing formed by tissues of both the funiculus and the outer integument; mature seed coat thin except for a part of the wing, consisting only of elongate cells of the outer epidermis of the testa and of walls of the other collapsed cells of the testa and tegmen.

Alzatea has six of the seven ordinal characteristics which we gave for the Myrtales (cf. Tobe & Raven, 1983a): (1) anther tapetum glandular, (2) ovule crassinucellate, (3) inner integument two-layered, (4) antipodals ephemeral, (5) endosperm formation of the Nuclear type, and (6) mature seed exalbuminous. The only disagreement is that *Alzatea,* like *Rhynchocalyx* (Tobe & Raven, 1984), has a micropyle formed by the inner integument alone instead of by both integuments. *Alzatea* is an exceptional member of the Myrtales in this respect.

Alzatea is also characterized by having a bisporic *Allium*-type embryo sac, a feature that is unknown elsewhere in Myrtales. Among other Myrtales, Penaeaceae and Onagraceae are characterized by unique embryo sac types, namely *Penaea*-type and *Oenothera*-type (cf. Tobe & Raven, 1983a, for review). All other Myrtales including not only *Axinandra* and *Rhynchocalyx* (which have been relegated to Crypteroniaceae together with *Alzatea*) but also Lythraceae (which may be related to *Alzatea*), have a monosporic *Polygonum*-type embryo sac (Tobe & Raven, 1983a, 1983b, 1984). Possession of an embryo sac type unknown elsewhere in the order seems strongly to suggest an isolated position of *Alzatea* within Myrtales. Embryological comparisons between *Alzatea* and other possibly related Myrtales are presented below using other features.

As regards the possibility of a relationship with *Axinandra,* with which *Alzatea* has been included as a member of an enlarged Crypteroniaceae (van Beusekom-Osinga & van Beusekom, 1975), *Alzatea* agrees with *Axinandra* in having a persistent anther epidermis and an ephemeral endothecium but differs from it in many other characters. In *Alzatea,* the ovule archesporium is multicelled; an endothelium is not formed; and the micropyle is formed by the inner integument alone. In contrast, in *Axinandra* the ovule archesporium is one-celled; a distinctive endothelium is formed; and the micropyle is formed by both integuments (Tobe & Raven, 1983b). In addition, the following point of difference may be mentioned: the seed wing is formed by tissues of both the funiculus and the outer integument in *Alzatea,* but it is formed by tissues of the funiculus alone in *Axinandra* (Tobe & Raven, 1983b). This, especially taken together with the fact that the embryo is situated centrally in the wing in *Alzatea,* basally in *Axinandra,* strongly suggests that the wings on the seeds of *Alzatea* and *Axinandra* are not homologous, and that this feature should not be used to link the two genera. In summary, too many dissimilarities to accept a mutual close relationship lie between *Alzatea* and *Axinandra.*

As regards a relationship with *Rhynchocalyx, Alzatea* agrees much more closely in its embryological features with this genus than with any other genus studied thus far. Shared characteristics include: anther epidermis persistent; endothecium ephemeral; ovule archesporium multicelled; micropyle formed by the inner integument alone; free endosperm nuclei scanty; and, finally, embryogenesis of the Onagrad type (Tobe & Raven, 1984). *Alzatea* differs from *Rhynchocalyx,* however, in the following respects: the septum between two microsporangia degenerates in *Alzatea* but is persistent in *Rhynchocalyx*; the radial elongation of nucellar subdermal cells surrounding megaspores does not occur in *Alzatea* but is characteristic of *Rhynchocalyx*; a hypostase is present in *Alzatea* but absent in *Rhynchocalyx*; the seed wing is formed by tissues of both the funiculus and the outer integument in *Alzatea* but it is formed by tissues of the funiculus alone in *Rhynchocalyx* (Tobe & Raven, 1984). Once again this suggests that the seed wing in *Alzatea* may not be homologous with that in *Rhynchocalyx,* and should not be used as evidence of relationship between these genera. Moreover, as we have seen, the embryo is situated centrally in its wing in *Alzatea*; in *Rhynchocalyx,* it is situated apically in the wing. The totality of similarities and dissimilarities, however, suggests that *Alzatea* is more closely related to *Rhynchocalyx* than to *Axinandra,* although *Alzatea* is still very distinct from and almost certainly not directly related to *Rhynchocalyx.*

As regards a possible relationship to Lythra-

ceae, *Alzatea* agrees with this family in having a multicelled ovule archesporium but differs from it in many respects. The anther epidermis is persistent in *Alzatea* but probably not in Lythraceae; the endothecium is ephemeral in *Alzatea* but seems to develop into fibrous thickenings in Lythraceae; starch grains are absent in the nucellus in *Alzatea* but present in Lythraceae (*Cuphea,* Hubert, 1896); the micropyle is formed by the inner integument alone in *Alzatea* but by both integuments in Lythraceae; the endosperm is scanty throughout seed development in *Alzatea,* much more abundant in Lythraceae (cf. Tobe & Raven, 1983a). Although we do not have complete enough information on the mature seed morphology and anatomy of Lythraceae to characterize the family fully, the points of difference just listed, in addition to the major difference in the embryo sac formation we have reported here, seem adequate to preclude the inclusion of *Alzatea* in Lythraceae on embryological grounds alone, thus supporting the conclusions of Graham (1984).

As regards the possibility of a relationship to Melastomataceae, which has recently been suggested on the basis of vegetative anatomy (van Vliet, 1975; van Vliet & Baas, 1975), *Alzatea* agrees with this family (only with the subfamily Melastomatoideae) in having a persistent anther epidermis and an ephemeral endothecium but differs from it in the following respects. Anther tapetal cells are two-nucleate in *Alzatea,* one-nucleate in Melastomataceae; the ovule archesporium is multicelled in *Alzatea,* one-celled in Melastomataceae; the micropyle is formed by the inner integument alone in *Alzatea,* by both integuments in Melastomataceae (cf. Tobe & Raven, 1983a). Thus embryological similarities between *Alzatea* and Melastomataceae are limited to anther wall characters alone whereas the dissimilarities include embryological features of many different kinds. *Alzatea* seems clearly to be much more distinct from Melastomataceae than from *Rhynchocalyx.*

In summary, evidence from the embryology of *Alzatea,* as well as from that of *Rhynchocalyx* (Tobe & Raven, 1984), clearly contradicts the broad definition of Crypteroniaceae to include both *Alzatea* and *Rhynchocalyx* proposed by van Beusekom-Osinga and van Beusekom (1975). *Alzatea* is distinct from all other Myrtales in having a bisporic *Allium*-type embryo sac. In addition, *Alzatea* differs from *Axinandra, Rhynchocalyx,* Lythraceae, and Melastomataceae in a considerable number of embryological characteristics in each case. These relationships strongly favor the establishment of a monotypic family Alzateaceae, standing apart from both Crypteroniaceae in a restricted sense and from Lythraceae, a treatment which is here proposed by Graham (1984), with support from Dahlgren and Thorne (1984) and from Johnson and Briggs (1984).

When compared embryologically with other Myrtales, *Alzatea* shares many more characteristics with *Rhynchocalyx* than with any other genus. Similarities with *Rhynchocalyx* are shown by the vegetative characters (such as stomatal type and overall wood anatomy), too, although a considerable number of points of difference with *Rhynchocalyx* in other vegetative features (such as cuticular texture, petiole anatomy, and vessel morphology) also remain (van Vliet, 1975; van Vliet & Baas, 1975). A relationship between *Alzatea* and *Rhynchocalyx* was likewise implied by their grouping as the only members of Crypteroniaceae subfamily Alzateoideae by van Beusekom-Osinga and van Beusekom (1975). *Rhynchocalyx* tends increasingly to be included in Lythraceae (van Vliet & Baas, 1975; Dahlgren & Thorne, 1984; Graham, 1984). Our recent study of the embryology of *Rhynchocalyx* suggests, however, that *Rhynchocalyx* is more distantly related to Lythraceae than might have been expected (Tobe & Raven, 1984). The fact that *Alzatea* has more similarities with *Rhynchocalyx* than with other Myrtales suggests that *Alzatea* and *Rhynchocalyx* are parallel descendants from a common ancestor, with which the modern Lythraceae possibly have a direct link. Our conclusion here agrees with that of Johnson and Briggs (1984), who, on the basis of their cladistic analysis, concluded that *Rhynchocalyx* was not directly related to Lythraceae but deserved to be assigned to a family of its own. We believe on the basis of the accumulating evidence that the similarities between *Alzatea, Rhynchocalyx,* Lythraceae (including Sonneratiaceae), and presumably Crypteroniaceae sensu stricto also are based on generalized ancestral features, not on derived ones indicative of direct relationship. The unambiguous conclusion seems to be that if any one of these groups deserves recognition at the family level, each of them does. The only distinctive embryological characteristic common to *Alzatea, Rhynchocalyx,* and Lythraceae is the possession of the multicelled ovule archesporium, which is unknown elsewhere in the order

except in one of the subfamilies of Lythraceae, Sonneratioideae (Tobe & Raven, 1983a). This shared characteristic seems to be suggestive of a relationship between these groups, although we still cannot evaluate the systematic significance of such an embryological character.

From the viewpoint of vegetative anatomy, *Alzatea* is the only Myrtalean genus that has a trilacunar nodal type, which is considered an ancestral rather than a derived feature (Baas, pers. comm. in Dahlgren & Thorne, 1984). The tricolporate pollen grains of *Alzatea* clearly are also an unspecialized, ancestral feature, thus contrasting with the undoubtedly derived heterocolpate grains of *Axinandra, Dactylocladus, Rhynchocalyx,* and many other Myrtales and the specialized and very unusual bilaterally flattened bisyncolporate grains of *Crypteronia* (Muller, 1975). But the persistent anther epidermis, the ephemeral (or non-fibrous) endothecium, and the bisporic *Allium*-type embryo sac, all of which are characteristic of *Alzatea,* are undoubtedly derived features. They do not suggest a direct relationship of *Alzatea* with any other group, however, and thus do not contradict the notion that it may have had a long, independent evolutionary history of its own.

We believe that the studies we have reported here underscore the utility of embryological features in elucidating the pathways of evolution within Myrtales. In order to fix the exact position of unique genera such as *Alzatea* and *Rhynchocalyx* better, comprehensive embryological studies will be required not only of Lythraceae and Melastomataceae (both of which have been studied only to a limited degree), but also of other genera, especially *Crypteronia* and *Dactylocladus,* which are unknown embryologically. When these results are available, embryological studies should be able to make an especially strong contribution to our understanding of this very distinct austral order of angiosperms, and to help to illuminate the relationships between its ancient evolutionary lineages.

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